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A decade of fish-killing *Prymnesium parvum* blooms in Texas: roles of inflow and salinity

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Fish-killing *Prymnesium parvum* blooms have occurred in south-central USA for at least ~30 years, with the last decade experiencing recurrent blooms of large magnitude. In the systems reported here, Lakes Possum Kingdom, Granbury and Whitney (Texas), *P. parvum* blooms were winter phenomena developing under conditions far from the growth optimum. Bloom thresholds of 10×10^6 cells L^{-1} were observed as a function of inflow and salinity for the period 2000−2009. In Lake Possum Kingdom, blooms occurred only when 7-day accumulated inflows were $<10 \times 10^6$ m^3 and salinities were >1.5 psu. For Lakes Granbury and Whitney, blooms occurred when 7-day accumulated inflows were $<20 \times 10^6$ m^3 and $<40 \times 10^6$ m^3, respectively, and salinities were >0.5 psu. Inflow to these lakes exceeded thresholds during the spring and early-summer months in 8 (Lake Possum Kingdom), 7 (Lake Granbury) and 6 (Lake Whitney) of the 10 years analyzed. Salinities typically exceeded these thresholds during the period of study prior to the spring of 2007. The spring of 2007 was a period of high precipitation, after which salinities were typically below thresholds. The linkage between incidence of *P. parvum* blooms, inflows and salinity is of concern because combined effects from human population increase and climate change could lead to periods of decreased inflow and increased salinity, which may then increase the frequency and magnitude of *P. parvum* blooms.

KEYWORDS: Haptophyte; fish-kill; bloom; hydraulic flushing; salinity

INTRODUCTION

Inflows and salinity have long been recognized as factors influencing phytoplankton community dynamics and structure (Ketchum, 1951, 1954). The magnitude and timing of inflows produce nutrient pulse and flushing loss variations that select for species adapted for these conditions, which in turn influence plankton community composition and productivity (Roelke *et al.*, 2003; Buyukates and Roelke, 2005; Miller *et al.*, 2008). Nutrient pulses and flushing losses associated with inflows also have been linked to the incidence of harmful algal blooms (Seliger *et al.*, 1970; Anderson and

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Stolzenbach, 1985; Paerl, 1988; Jacoby *et al.*, 2000; Moustaka-Gouni *et al.*, 2006; Mitrovic *et al.*, 2008), including a toxic bloom of *Prymnesium parvum* (Roelke *et al.*, 2010a).

Prymnesium parvum, a haptophyte alga, occurs worldwide. It is tolerant of large variations in temperature and salinity, and is capable of forming large fish-killing blooms (Lundholm and Moestrup, 2006; Baker *et al.*, 2007, 2009; Southard *et al.*, 2010). In the USA, the first recorded *P. parvum* bloom occurred in 1985 in a semi-arid region of the country (Pecos River, Texas) (James and De La Cruz, 1989). Since then, the incidence of *P. parvum* blooms dramatically increased in the USA, where the organism has invaded lakes and rivers throughout southern regions and most recently into northern regions (Fig. 1). *Prymnesium parvum* blooms typically occur in aquatic systems that are eutrophic and brackish (Kaartvedt *et al.*, 1991; Guo *et al.*, 1996; Roelke *et al*, 2007a, 2010a, b; Hambright *et al.*, 2010).

Many factors likely contribute to *P. parvum* bloom formation. They include production of chemicals toxic to grazers (Granéli and Johansson, 2003; Tillmann, 2003;

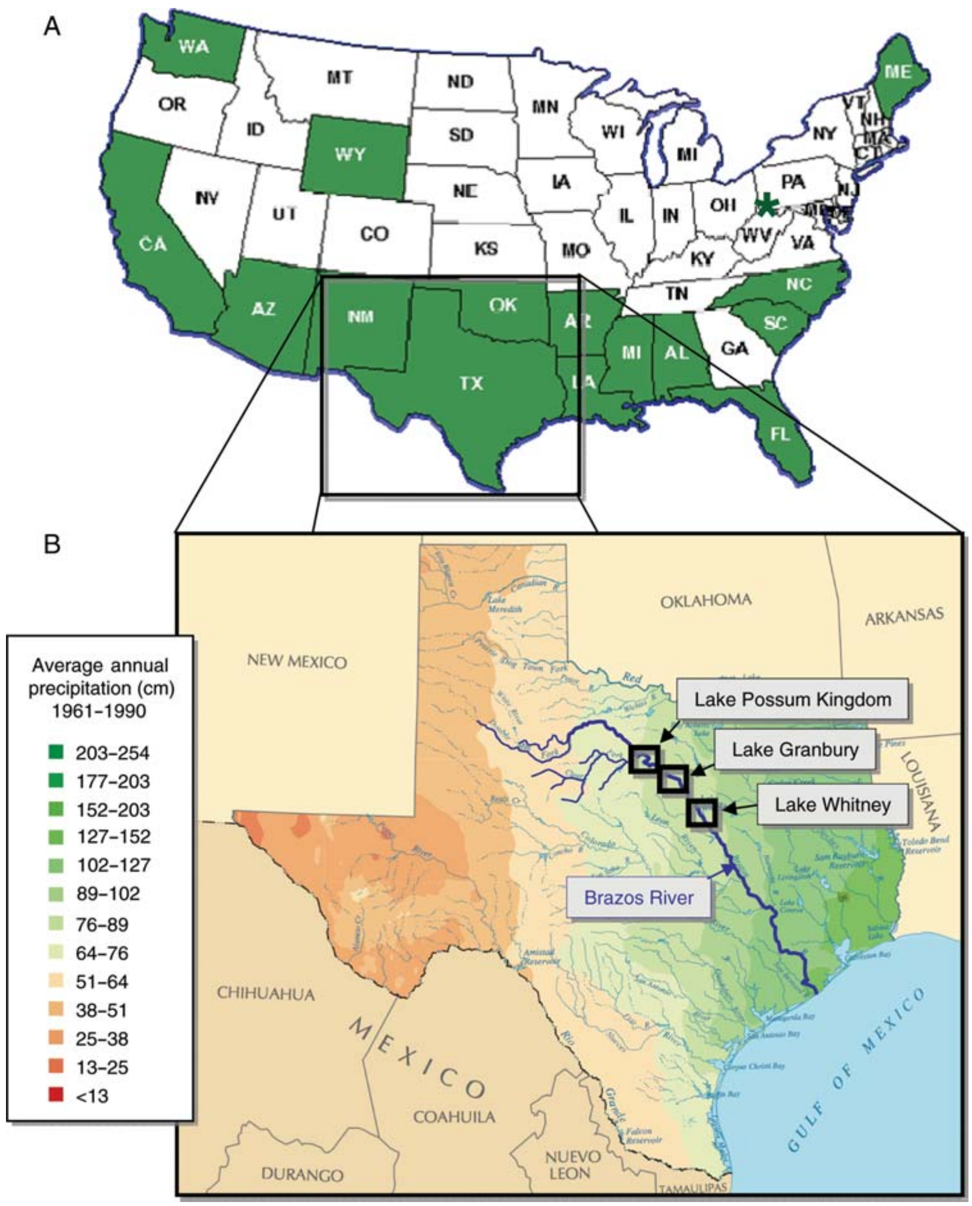

Fig. 1. States in the USA where *Prymnesium parvum* was confirmed (modified from Sager *et al.*, 2008) where the asterisk indicates the most recent northward spread of this invasive species (**A**), and the east–west precipitation gradient across Texas (**B**) (from The National Atlas of the United States of America, US Department of the Interior and US Geological Survey). The three lakes studied for this research included Lakes Possum Kingdom, Granbury and Whitney (Texas), situated along the Brazos River in an area receiving ~90 cm year^{-1} of rainfall.

Barreiro *et al.*, 2005; Michaloudi *et al.*, 2009; Brooks *et al.*, 2010), use of alternative energy and nutrient sources through mixotrophy and saprophytic nourishment (Nygaard and Tobiesen, 1993; Skovgaard and Hansen, 2003; Lindehoff *et al.*, 2009), suppression of competitors through allelopathy (Fistarol *et al.*, 2003, 2005; Granéli and Johansson, 2003; Roelke *et al.*, 2007a; Errera *et al.*, 2008) and resistance to the allelopathic effects of other algae (Suikkanen *et al.*, 2004; Tillmann *et al.*, 2007). Factors that negatively influence *P. parvum* population density might include grazing by toxin-resistant zooplankton and pathogenic effects of virus (Schwierzke *et al.*, 2010). In addition, some cyanobacteria may inhibit *P. parvum* blooms (Grover *et al.*, 2010; Roelke *et al.*, 2010b; James *et al.*, in review).

In regards to inflow and salinity, both have been shown as important factors influencing *P. parvum* population dynamics and reproductive growth rates. A recent study documenting the entire seasonal *P. parvum* bloom cycle in a Texas lake found that cell loss through hydraulic flushing during a period of high inflow, along with cessation of toxin production associated with nutrient loading, was the primary mechanism terminating the bloom (Roelke *et al.*, 2010a). In regards to salinity, using a Texas strain of *P. parvum* (UTEX LL 2797), the optimal salinity for reproductive growth was determined to be 22 psu. At 10°C, a temperature representative of winter conditions when blooms are most common in the region, growth rates decreased ~10-fold (from ~0.2 to 0.02 day^{-1}) as salinity decreased from the optimum to levels found in Texas lakes (Baker *et al.*, 2007, 2009). Baker *et al.* (Baker *et al.*, 2007, 2009) also suggested that small variations in salinity at low levels determine whether reproductive growth is possible.

Here, we further investigate the role of inflow and salinity as they influence the occurrence of *P. parvum* blooms. We focus on three Texas lakes located along the Brazos River, where observations of blooms have occurred during winter months since late 2000–early 2001. Quantitative sampling commenced in 2002 and 2003, and we include data through 2009.

Study region

The Brazos River flows southeast across Texas (USA), spanning a rain gradient from the arid western regions of the state (averaging ~13–26 cm year^{-1}) to the moister eastern region, with an average of ~155 cm year^{-1} (Fig. 1). This study focused on the three uppermost large reservoirs of the Brazos River; Lakes Possum Kingdom (centered at 32.87°N, 98.50°W, construction completed in 1941), Granbury (32.40°N, 97.76°W, 1969) and Whitney (32.00°N, 97.43°W, 1951) (Fig. 2). All three lakes are located in the watershed region receiving ~90 cm year^{-1} of rainfall. Lakes Possum Kingdom and Granbury are sinuous with shorelines that follow the submerged river channel, but the lakes differ in their morphometry and catchment area (see Handbook of Texas Online, 2010). Lake Possum Kingdom has the largest volume of the three lakes, with a capacity of 893×10^6 m^3. It has a surface area of 80 km^2, average depth of ~11 m and a 36 337 km^2 drainage area. Lake Granbury has the smallest volume of the three, with a capacity of 188×10^6 m^3. It receives inflows from Lake Possum Kingdom and runoff from the increased catchment area. Its surface area, average depth and total drainage area are 34 km^2, ~5 m and 41 732 km^2. The capacity, area and average depth of Lake Whitney are 467×10^6 m^3, 95 km^2 and ~5 m, respectively. Lake Whitney receives inflows from Lake Granbury and the increased catchment area (45 644 km^2 total). Further characterizations of these lakes can be found in Roelke *et al.* (Roelke *et al.*, 2007a, 2010a) and Schwierzke *et al.* (Schwierzke *et al.*, 2010).

METHOD

This study focused on the role of river inflow and in-lake salinity as they relate to *P. parvum* population density. A bloom was defined as being when *P. parvum* population density exceeded 10×10^6 cells L^{-1}, a level above which toxicity and fish kills are frequently observed. Data were compiled from monitoring activities of Texas A&M University, Brazos River Authority and Texas Parks and Wildlife Department. Locations of sampling stations were system-wide and encompassed shore-based and open-lake locations for each lake (Fig. 2). Sampling frequency was generally weekly to bi-weekly during the late-fall through early spring (the time of year when *P. parvum* blooms develop and terminate), and monthly to quarterly for the remaining period. Quantitative sampling commenced in Lake Possum Kingdom during 2002 and began in 2003 for Lakes Granbury and Whitney. Prior to this, *P. parvum* population densities were not quantified. Data from 1556 sampling events were compiled from all three lakes, i.e. 371 events in Lake Possum Kingdom, 878 in Lake Granbury and 307 in Lake Whitney.

Estimations of *P. parvum* population density in surface waters were achieved using either a settling technique or a hemacytometer, with personnel from all institutes performing the counts. For the settling technique (Utermöhl, 1958), in most cases, a 100 mL phytoplankton sample was collected from each station at ~0.5 m depth and preserved using glutaraldehyde, 5% v/v and

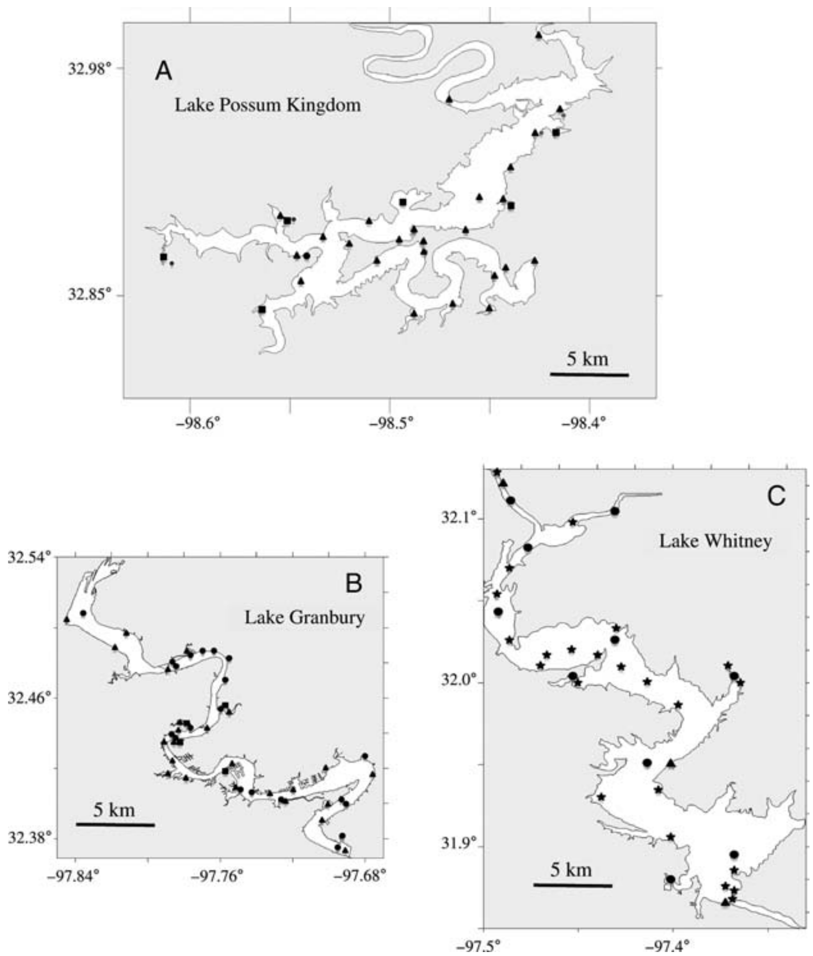

Fig. 2. Maps of Lakes Possum Kingdom (**A**), Granbury (**B**) and Whitney (**C**) showing the location of sampling stations. Circles (•) represent stations that were sampled monthly for periods spanning multiple years by Texas A&M University, stars (★) represent stations that were sampled weekly during periods of bloom and monthly otherwise for a period spanning two years (Texas Parks and Wildlife Department) and squares (■) and triangles (▲) represent stations that were sampled monthly or quarterly over periods spanning several years by Brazos River Authority and Texas Parks and Wildlife Department.

then a 1 mL subsample was settled for 24 h. Randomly selected fields-of-view were then counted until >200 *P. parvum* cells were enumerated (20 to 40 fields-of-view). Sample stations designated with a "circle" and "star" on Fig. 2 were enumerated following settling techniques. For the less sensitive hemacytometer technique, live samples were analyzed repeatedly until counting thresholds of 0.37×10^6 cells L^{-1} ("triangle") and 2×10^6 cells L^{-1} ("square") were attained.

Daily discharges from the Brazos River were measured at the following upstream locations: South Bend, USGS Station Number 08088000 (Lake Possum Kingdom); Dennis, USGS Station Number 08090800 (Lake Granbury) and Glen Rose, USGS Station Number 08091000 (Lake Whitney). Salinities were measured during sampling using water quality multiprobes (Quanta, Hydrolab) and refractometers.

Simple correlations using linear-, exponential- and power-fit functions (Kaleidagraph, v.4.03), and multiple regression analysis (Matlab, v.7.5.0.338) were performed between *P. parvum* population density, inflow and salinity. We used correlation analyses to estimate the percent variability in *P. parvum* population density explained by either inflow or salinity (based on R^2), and the multiple regression analysis enabled us to simultaneously compare the relative roles of inflow and salinity as they affect *P. parvum* population density (based on the weighting coefficients). For inflows, we used 7-day, 10-day, 30-day and 365-day cumulative inflow prior to each sampling date. The 7-day cumulative inflows showed the best relationships and only those results are reported here.

To better relate inflow magnitudes to the specific growth rate of *P. parvum*, we estimated daily system flushing rates during the time of peak flows. For this purpose, system flushing rates were estimated by dividing the daily inflow from the Brazos River by the lake volume.

RESULTS

After the 1985 Pecos River event (James and De La Cruz, 1989) when *P. parvum* was first linked to a fish kill in this region, and multiple smaller-sized fish kills in the Brazos River area and elsewhere during the following decade (Southard *et al.*, 2010), the first large-scale, fish-killing *P. parvum* blooms in Texas occurred in multiple systems along the Brazos River during the late fall 2000–early spring 2001. In the Brazos River Basin, the blooms first appeared in Lake Possum Kingdom, then in the state fish hatchery between Lakes Possum Kingdom and Granbury, next in Lake Granbury and eventually reached Lake Whitney. This stretch of the Brazos River is ~120 km. Several fish kills resulted from these *P. parvum* blooms (Southard *et al.*, 2010), but observations of population densities and bloom spread downstream are largely anecdotal.

In the years following the 2000–2001 blooms (when quantitative sampling commenced) until the early spring of 2007, fish-killing *P. parvum* blooms were recurrent winter phenomena in all three lake systems, lasting ~2 months (Fig. 3). The timing of these blooms was no longer sequential, as it was during the 2000–2001 period, but instead concurrent. Bloom density maxima increased further down the watershed with maximum bloom densities of ~40–60 × 10^6 cells L^{-1} in Lake Possum Kingdom, ~80–100 × 10^6 cells L^{-1} in Lake Granbury and ~140–170 × 10^6 cells L^{-1} in Lake Whitney. During these events, waters took on a golden color, surface foam was observed and dead fish were seen throughout the affected lakes (Fig. 4). After early-spring 2007, recurrent *P. parvum* population maxima still occurred during the late-fall through early-spring months. Maximum population densities were lower, however, typically reaching ~10 × 10^6 cells L^{-1} for Lake Possum Kingdom, ~20–60 × 10^6 cells L^{-1} for Lake Granbury and ~10–30 × 10^6 cells L^{-1} for Lake Whitney. During this period, fish kills were smaller and localized within each lake.

As is typical for this region, rains and associated in-stream flows were highest during the early-spring through early-summer months (Fig. 3). Lake inflows increased in magnitude further down the watershed, presumably because of the increased area of catchment. The spring of 2007 was the wettest period of this data record, with peak inflows attaining ~60 × 10^6 m^3 day^{-1} for Lake Possum Kingdom and ~120 × 10^6 m^3 day^{-1} for Lakes Granbury and Whitney. Whole system flushing rates during peak inflows in the spring of 2007 were 0.08, 0.7 and 0.3 day^{-1} for Lakes Possum Kingdom, Granbury and Whitney. Dry years occurred earlier in the data record where inflows were barely discernable at times. For Lake Possum Kingdom, located highest in the watershed, 2008 and 2009 were also dry

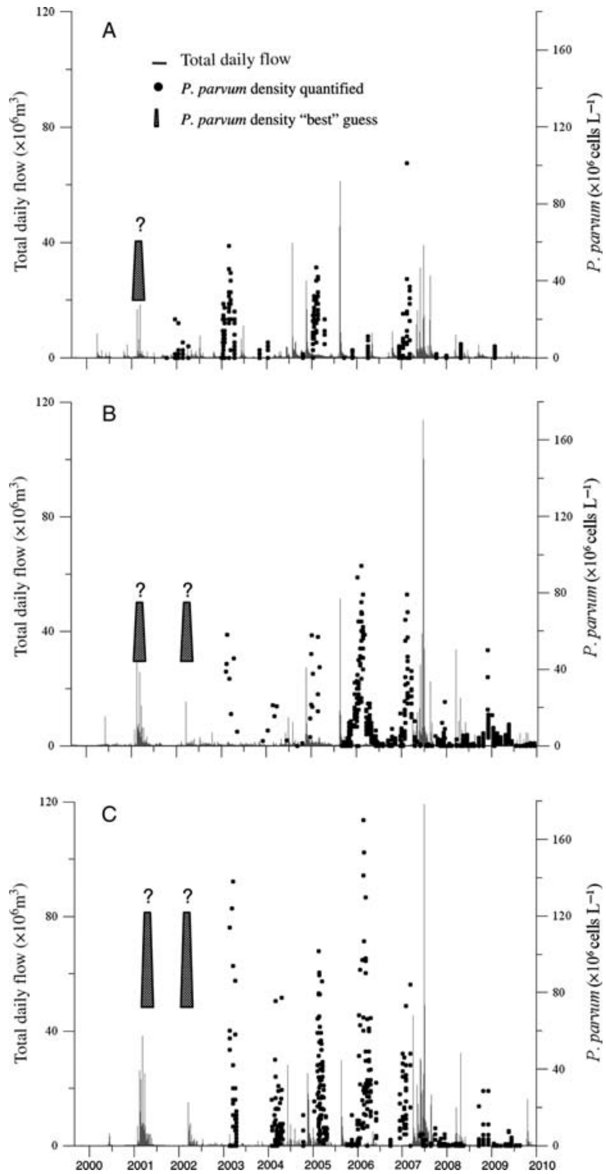

Fig. 3. Recurrent blooms of *Prymnesium parvum* and daily inflows for a period spanning 2000 through 2009 for Lakes Possum Kingdom (**A**), Granbury (**B**) and Whitney (**C**). During late 2000–early 2001 for Lake Possum Kingdom, and 2001–2002 for Lakes Granbury and Whitney, population densities were approximated from anecdotal information (indicated with a '?'). Otherwise, population densities were quantified. Inflow data were obtained from US Geological Survey.

Fig. 4. Features of fish-killing *Prymnesium parvum* blooms. During periods of high *P. parvum* population density waters take on a characteristic golden color (**A**). Usually when this color is apparent, waters are toxic to fish and large die-offs result (**B** and **C**) (photographs courtesy of Brazos River Authority and Texas Parks and Wildlife Department).

years. For Lakes Granbury and Whitney, 2009 was a dry year.

Cumulative inflow for the 7-day period prior to each sampling time showed that higher inflows resulted in lower population densities (Fig. 5). Although more observations of *P. parvum* population density at higher inflows are needed, inflow bloom-thresholds (defined as 10×10^6 cells L^{-1}) were apparent, and they varied for each lake, i.e. $\sim 10 \times 10^6$ m^3 day^{-1} for Lake Possum Kingdom (corresponding to a whole system flushing rate of 0.01 day^{-1}), $\sim 20 \times 10^6$ m^3 day^{-1} (0.12 day^{-1}) for Lake Granbury and $\sim 40 \times 10^6$ m^3 day^{-1} (0.10 day^{-1}) for Lake Whitney. Inflow to these lakes exceeded thresholds during the spring and early-summer months. For Lake Possum Kingdom, this occurred during 8 of the 10 years analyzed. For Lakes Granbury and Whitney, this occurred in 7 and 6 of the years, respectively. While an inflow threshold was observed, above which *P. parvum* populations did not accumulate, monotonic trends were not seen. Linear, power and exponential functions used to correlate 7-day cumulative inflow and *P. parvum* population densities were poor. Using data pooled from all three lakes, models only explained 2%, 1% and 1% of the total variability (equations not shown). Similar findings were obtained when lakes were analyzed separately.

Reports of salinity during the 2000–2001 bloom period were as high as 4 psu in Lake Possum Kingdom (J. Glass, personal communication). Our records for salinity started in 2004 and typically showed annual maxima of $\sim 2-3$ psu for these three lakes prior to the early-spring of 2007 (Fig. 6). After the wet season of 2007, annual maxima were typically $\sim 1-2$ psu. There appeared to be a salinity threshold below which *P. parvum* blooms did not occur. At salinities below ~ 1.5 psu for Lake Possum Kingdom and 0.5 psu for Lakes Granbury and Whitney, population densities of *P. parvum* were $< 10 \times 10^6$ cells L^{-1} (Fig. 7). There was one exception in Lake Whitney where *P. parvum* population density exceeded bloom level at low salinity. When data from all three lakes were pooled, linear [equation (1)], power [equation (2)] and exponential functions [equation (3)] used to correlate salinity and *P. parvum* population densities explained 41%, 40% and 34% of the total variability in this data record. Model equations were:

$$[\mathrm{pop}] = 12.11[\mathrm{sal}] - 4.86 \qquad (1)$$

$$[\mathrm{pop}] = 1.84[\mathrm{sal}]^{2.01} \qquad (2)$$

$$[\mathrm{pop}] = 0.21e^{1.93[\mathrm{sal}]} \qquad (3)$$

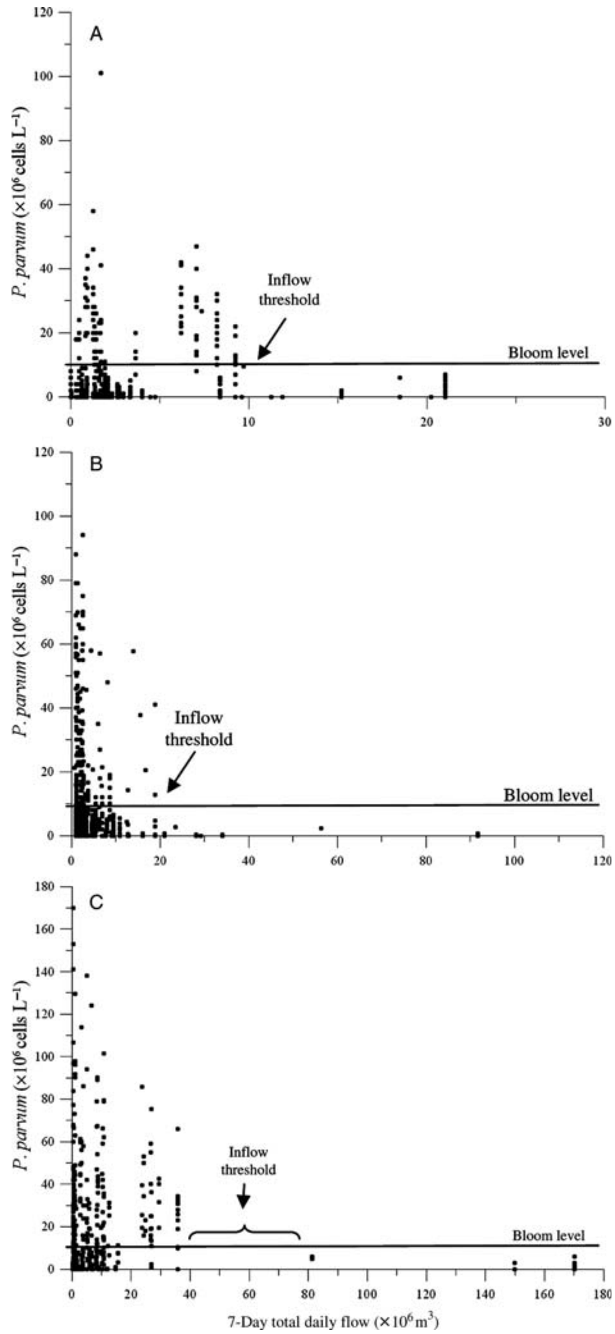

Fig. 5. *Prymnesium parvum* population density plotted against the cumulative inflow over the 7-day period prior to the date of sampling for Lakes Possum Kingdom (**A**), Granbury (**B**) and Whitney (**C**). Population densities greater than 10×10^6 cells L^{-1}, the defined bloom level, occurred when 7-day accumulated inflows were $<10 \times 10^6$ m^3 for Lake Possum Kingdom, $<20 \times 10^6$ m^3 for Lake Granbury and conservatively $<40 \times 10^6$ m^3 for Lake Whitney. These bloom inflow-thresholds corresponded to system flushing rates of 0.01, 0.12 and 0.10 day^{-1}.

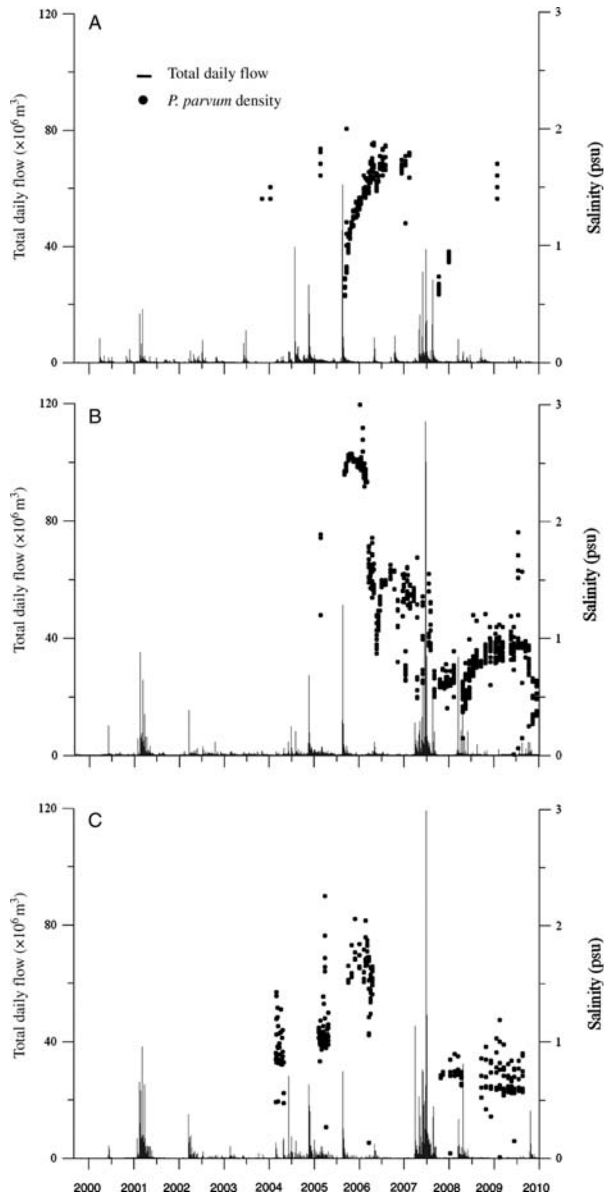

Fig. 6. Salinity and inflows for a period spanning 2000 through 2009 for Lakes Possum Kingdom (**A**), Granbury (**B**) and Whitney (**C**). Prior to the wet spring of 2007, annual salinity maxima typically ranged from 2–3. After this wet period, annual salinity maxima typically ranged between 1–2.

Similar findings were obtained when lakes were analyzed separately (data not shown). The multiple linear regression [equation (4)] using the 7-day cumulative inflow and salinity indicated that salinity more strongly influenced *P. parvum* population density than inflow, where the model was:

$$[\text{pop}] = 0.02[\text{inflow}] + 8.96[\text{sal}] - 3.78 \qquad (4)$$

However, this model only explained ~11% of the variance in *P. parvum* population density.

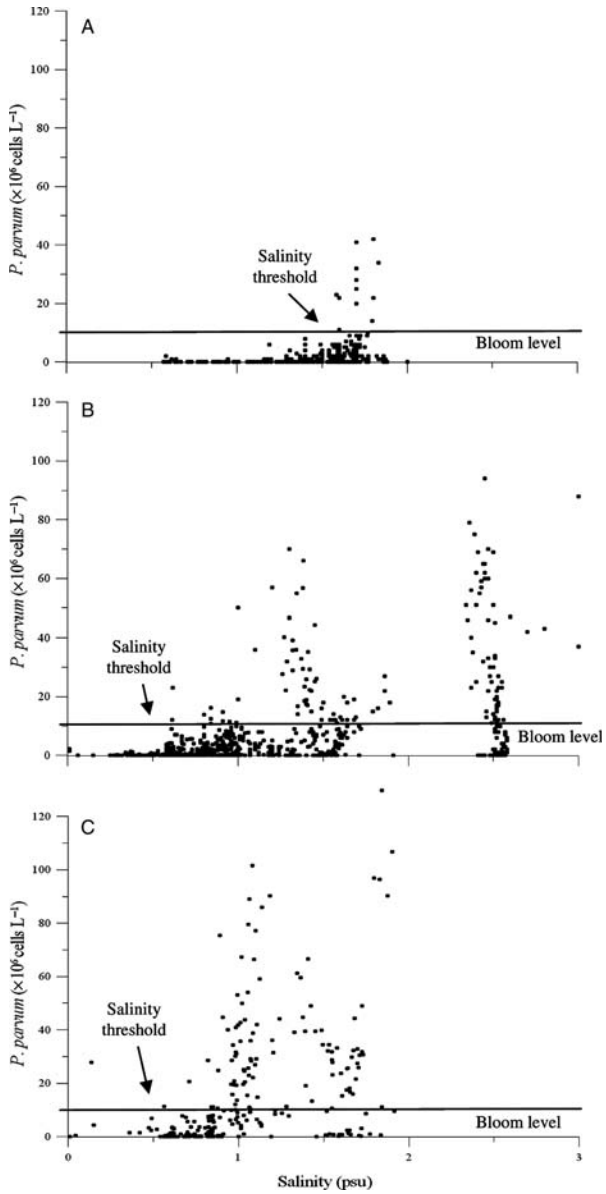

Fig. 7. *Prymnesium parvum* population density plotted against salinity for Lakes Possum Kingdom (**A**), Granbury (**B**) and Whitney (**C**). Population densities greater than 10×10^6 cells L^{-1}, the defined bloom level, occurred when salinities were >1.5 for Lake Possum Kingdom, and >0.5 for Lakes Granbury and Whitney.

DISCUSSION

Prymnesium parvum in Texas appears to be the result of invasion (Lutz-Carrillo *et al.*, 2010). Our data suggest that invading *P. parvum* established quickly in lakes downstream from early bloom events. For example, fish-killing blooms appeared sequentially down the watershed after they were first noticed in late 2000–early 2001. However, between 2004 and 2007, fish-killing blooms were concurrent, suggesting that immigration of *P. parvum* from upstream sources was no longer necessary for bloom initiation. The apparent rapid spread of *P. parvum* across the southern USA, and now with fish-killing blooms in northern areas (e.g. West Virginia and PA, USA), also suggests that this species is an effective invader.

Paradoxically, our documentation of this invasive species shows that the recurrent blooms occurred under conditions far removed from the growth optimum. Laboratory studies using a Texas strain of *P. parvum* (UTEX LL 2797) showed optimal reproductive growth rates of ~0.8 day^{-1} when salinity and temperature were 22 psu and 27°C (Baker *et al.*, 2007, 2009). Using the equation from Baker *et al.* (Baker *et al.*, 2009) and winter temperatures of ~10°C, maximum reproductive growth rates were estimated to be ~0.1 day^{-1} for the period prior to early-spring 2007, when annual salinity maxima ranged from 2 to 3 psu. In other words, blooms occurred when reproductive growth was stressed by low salinity and temperature. In the absence of significant loss factors, such as grazing, these low reproductive growth rates can lead to blooms of high population density, as was demonstrated using a simplified biophysical model depicting *P. parvum* bloom dynamics in Lake Granbury (Roelke *et al.*, 2010a). Production of grazing-inhibiting toxins would facilitate this condition, and appears to be the case for *P. parvum*, which produces greater amounts of grazing-inhibiting toxin when stressed (Uronen *et al.*, 2005; Granéli and Salomon, 2010).

Prymnesium parvum blooms in these lakes were vulnerable to large inflow events because they occurred during a time of year when maximum reproductive growth rates were low. Thus, it is not surprising that *P. parvum* blooms only developed when inflows were below critical levels. In addition, blooms ceased when inflows exceeded these inflow bloom-thresholds during early-spring through early summer months. Estimated winter reproductive growth rates during bloom years (~0.1 day^{-1}) were similar to whole system flushing levels estimated at the inflow thresholds for Lakes Granbury and Whitney, 0.12 and 0.10 day^{-1}, respectively. This is consistent with observations from other systems where hydraulic flushing influenced plankton dynamics and the incidence of blooms (Jacoby *et al.*, 2000; Moustaka-Gouni *et al.*, 2006; Mitrovic *et al.*, 2008; Roelke *et al.*, 2010a). High inflows were not a requirement for bloom decline, however, as blooms ended with only modest inflows during years 2003, 2005 and 2006.

Inflow bloom-thresholds varied between lakes. Most notably, Lake Possum Kingdom required much less inflow to suppress *P. parvum* populations, where the corresponding system flushing rate was 0.01 day^{-1}.

Flushing thresholds were an order of magnitude greater for Lakes Granbury and Whitney. Differing thresholds likely stemmed from morphometric variations between systems. For example, Lake Possum Kingdom has a larger volume than Lakes Granbury and Whitney, and is nearly twice as deep. However, it is most likely not well mixed vertically, and flushing events may primarily affect surface waters. Consequently, the inflow required to flush a surface bloom from the system would be lower. Similarly, Lake Possum Kingdom is elongated and sinuous, and likely is not well mixed longitudinally. Inflows needed to flush a smaller water mass would also be lower than those required to flush the system.

Another factor concerning inflow bloom-thresholds pertains to cove presence and connectivity. In a lake north of our study area, *P. parvum* population densities were much higher in a disconnected cove compared to those of the open lake (Hambright *et al.*, 2010). Coves might harbor seeding *P. parvum* populations and serve as hydraulic storage zones. Volume exchange rates between storage zones and open waters were shown to influence the magnitude of inflow required to flush blooms from a system (Reynolds, 1990; Grover *et al.*, 2009, in press). It is likely that dendritic lakes may require higher inflows to terminate *P. parvum* blooms, though analysis of cove connectivity in these lakes is beyond the scope of the present research.

High inflows need not terminate blooms through hydraulic flushing. For example, toxin production by the Texas strain of *P. parvum* is sensitive to nutrient pulses (Grover *et al.*, 2007; Roelke *et al.*, 2007a; Errera *et al.*, 2008). In Lake Whitney, termination of a bloom was observed coinciding with an inflow event where the lake level rose, but no out-flow occurred. The *P. parvum* population declined 52%, where direct dilution accounted for ~30% of this decrease, and toxicity was completely removed (Schwierzke-Wade *et al.*, in review). Without the advantages imparted to *P. parvum* under stressful conditions (in this case, low nutrient concentrations), this bloom did not re-establish. It is likely that increased nutrient loading associated with inflows during 2003, 2005 and 2006 contributed to these bloom declines.

When comparing *P. parvum* population dynamics from the periods before and after the high inflow events of early-spring 2007, the incidence of blooms appeared sensitive to small variations in salinity. For example, only when annual salinity maxima reached 2–3 psu did system-wide high population density blooms occur. These blooms were accompanied by extensive fish-kills (see Southard *et al.*, 2010). When annual salinity maxima ranged from 1 to 2 psu, maximum *P. parvum* population densities were reduced to ~30% of previous levels, and fish kills were small and localized. The higher maximum reproductive growth rates estimated prior to the early-spring of 2007 likely contributed to the higher population densities at that time. Shifts in plankton community dynamics and structures that are sensitively dependent on environmental conditions were previously documented with bloom-forming flagellates and other nuisance taxa (Buskey *et al.*, 1998; Roelke *et al.*, 2007b; Shatwell *et al.*, 2008).

Interestingly, salinity bloom-thresholds varied between lakes. Blooms occurred in Lake Possum Kingdom only when salinity was >1.5 psu and in Lakes Granbury and Whitney when salinity was >0.5 psu. Inorganic nutrient concentrations were similar between these lakes during the periods of bloom development (Roelke *et al.*, 2007a, 2010a; Schwierzke *et al.*, 2010), so differential nutrient concentrations did not likely affect thresholds. It may be that plankton community sensitivity to salinity varied in these lakes. Due to its higher position in the watershed, the plankton of Lake Possum Kingdom is likely exposed to greater salinity variations naturally. Consequently, the plankton community there may be more tolerant to higher salinities. It may be that less-stressed plankton communities are more resistant to *P. parvum* blooms, which in the case of Lake Possum Kingdom, might lead to a greater salinity bloom-threshold.

Relationships between *P. parvum* population density, inflow and salinity were not monotonic. Instead, large ranges in *P. parvum* population densities were observed when inflows were lower and salinities were higher. In other words, lower inflows and higher salinities alone did not indicate *P. parvum* population densities would be high. Other factors not accounted for during our study were probably important. These may include competition for resources (Baker *et al.*, 2009), allelopathic effects from chemicals produced by *P. parvum* (Fistarol *et al.*, 2003, 2005; Granéli and Johansson, 2003; Michaloudi *et al.*, 2009), sensitivity of *P. parvum* to chemicals produced by other algae (Grover *et al.*, 2010; Roelke *et al.*, 2010b; James *et al.*, in review), use of alternative energy and nutrient sources through mixotrophy and saprophytic nourishment (Nygaard and Tobiesen, 1993; Skovgaard and Hansen, 2003; Lindehoff *et al.*, 2009), grazing inhibition (Granéli and Johansson, 2003; Tillmann, 2003; Michaloudi *et al.*, 2009; Brooks *et al.*, 2010) and grazing by toxin-resistant taxa and infection by virus (Schwierzke *et al.*, 2010). All of these processes influence *P. parvum* population dynamics to varying degrees and are not solely a function of inflow and salinity. So, it is not surprising that complex patterns and high variability in *P. parvum* population density were observed over the ranges of inflow and salinity recorded in this study.

In summary, *P. parvum* blooms (and annual population maxima for the period after early-spring 2007) were recurrent winter phenomena in this area of the south-central USA. Bloom initiation and development only occurred at a time of year when inflows were low, and large fish-killing blooms occurred only when salinity was higher. Bloom termination followed high inflow events, likely through direct flushing of cells and indirect physiological affects. This linkage between incidence of *P. parvum* blooms, inflows and salinity raises concern because sequestration of water continues to increase in this area with rising human population. Combined with variations in precipitation and evaporation predicted from climate change, flows in this area may decrease by 60% (Cai and McCarl, 2009). Though not the focus of climate change models, it is likely that increased evaporation rates associated with regional warming will also result in higher salinity. Consequently, both human population increase and climate change may lead to an increased incidence of *P. parvum* blooms.

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